An oceanographic characterization of swordfish (Xiphias gladius) longline fishing grounds in the springtime subtropical North Pacific

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ABSTRACT

During January-May, surface manifestation of multiple, individual basin-scale fronts accentuate the central North Pacific Subtropical Frontal Zone (STFZ) system. The most prominent of these fronts are climatologically located at 32°-34°N and at 28°-30°N latitudes [herein nominally referred to as the 'Subtropical Front' (STF) and the 'South Subtropical Front' (SSTF), respectively], although considerable interannual variability in both position and intensity is observed. This seasonally dynamic system is also the region typically targeted by the Hawaii-based swordfish (Xiphias gladius) longline fishing fleet, where the presence, position, and strength of the convergent fronts are believed to play a key role with regard to the catch and catch rates of swordfish. Information furnished by a recent series of meridional hydrographic surveys and concurrent satellite remote sensing data elucidate structural patterns and coupling of the physics and biology associated with these fronts. This enables a re-characterization of the spring North Pacific STFZ and offers new insight into the seasonal variability of the phytoplankton dynamics in the subtropical North Pacific.

On synoptic time scales, geographical positioning of the fronts may be systematically identified through surface outcropping of diagnostic thermohaline isopleths and therefore readily discerned from both shipboard surveys and by spaceborne sensors. The STF during spring can be characterized by the surface expression of the 34.8 isohaline and the 17°C isotherm within the frontal gradient, Biologically, the STF marks the transition from low chloropigment (chlorophyll + phaeopigments), nutrient-depleted surface waters to the south to a more productive regime to the north. To the south, the 20°C and 35.0 surface isotherm and isohaline, respectively, are characteristically embedded in the thermohaline gradients associated with the SSTF. A sharp increase in depthintegrated chloropigment is also observed at the SSTF and is ascribed to an increase in the concentration and thickness of the subsurface chloropigment maximum (SCM) prompted by the shoaling of the nutricline with the thermocline structure into the euphotic zone.

Key words: chloropigments, mesoscale variability, physical-biological coupling, satellite altimetry, Subtropical Front, *Xiphias gladius*

INTRODUCTION

In the early 1990s, a surface longline fishery for swordfish, *Xiphias gladius*, began operating in the central North Pacific waters north of the Hawaiian Archipelago (Ito *et al.*, 1998). While other international fisheries targeting swordfish concentrated their efforts in regions of high productivity, e.g. upwelling eastern boundary systems (Sakagawa, 1989), productivity of the oligotrophic open ocean fishing grounds frequented by the Hawaii-based fleet paled by comparison. Nevertheless, landings by the Hawaii-based fishery exceeded 6000 metric tons at its highest levels (Ito & Coan, 1999).

Prior studies have suggested that the presence and detection of oceanic fronts by the fleet can be instrumental in fishery performance, i.e. catch per effort for swordfish (Podestá *et al.*, 1993; Bigelow *et al.*, 1999) as

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25°N

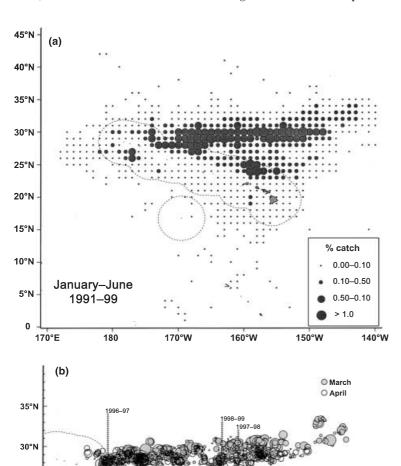
20°N

180

well as other highly migratory species, e.g. albacore tuna (Laurs & Lynn, 1977; Laurs *et al.*, 1984). For pelagic predators, convergent fronts represent regions of forage accumulation (Fiedler & Bernard, 1987; Olson *et al.*, 1994).

The region occupied by the Hawaii-based swordfish fleet is oceanographically referred to as the Subtropical Frontal Zone (STFZ) with peak fishing activity occurring during the winter–spring months (Fig. 1a). During this time of the year, multiple, large-scale semipermanent fronts can be found within the frontal zone; the two most prominent, the Subtropical Front (STF) and the South Subtropical Front (SSTF), climatologically located at 32°–34°N and at 28°–30°N latitudes, respectively (Roden, 1972, 1980, 1981, 1991). Concentration of thermohaline gradients in

the STFZ results from convergence and deformation of the Ekman flow (Roden, 1980) to the distribution of surface momentum and heat flux forcing (Kazmin & Rienecker, 1996). Because of the incomplete balance that exists between the temperature and salinity gradients, fronts in the STFZ exhibit moderate to significant density gradients, the strongest to the south (subtropics) diminishing northward with poleward cooling of surface waters. On synoptic time scales, pervasive mesoscale (10-100 km) processes in the form of meanders, eddies, jets, etc. are typically seen embedded within the fronts dominating the flow field. The fronts and resultant deformation of near surface gradients give rise to a highly dynamic baroclinic flow field and fluctuations in sea level height whose surface expressions are readily measured by satellite altimeters.



165°W

150°W

>30 swordfish per set

Figure 1. (a) Swordfish (Xiphias gladius) harvest (%) for the Hawaii-based commercial longline fishery by 1° latitude × 1° longitude statistical areas and (b) NOAA R/V Townsend Cromwell meridional survey tracks (1996–2000) and swordfish monthly catches per confidential set during March–April 1996–1999. All catch data are from the Federal longline logbook program (Ito et al., 1998).

The prevailing perception of the biological response to the physical STFZ environment has principally been borne from extensive works of the FIONA and CLIMAX programs (Hayward *et al.*, 1983; Hayward & McGowan, 1985; Venrick, 1988, 1990a,b, 1993). Most of this characterization has been formulated from series of summer sampling and of the highly stratified conditions typifying the region during these months of strong insolation.

In this paper, we present a renewed physical–biological characterization of the winter–spring North Pacific STFZ based on the results from a number of frontal crossings by ship and concurrent monitoring by multiple satellite sensors. We provide a new perspective of a highly dynamic region whose biological signature is defined not only by response to physical forcing of the seasonal large-scale frontal manifestation but also by the pervasive field of mesoscale perturbations.

METHODS

Because of the highly dynamic nature of the STFZ fishing grounds on varying temporal and spatial scales, a multiplatform approach involving satellite remote sensing and *in situ* shipboard surveys was undertaken (Table 1). Satellite mounted sensors provide near real-time synoptic data coverage on a large (basin) scale and insight into temporal variability. *In situ* shipboard surveys describe processes that occur on the local- and meso-scale and provide the information necessary for ground truthing and subsurface interpretation of surface-limited, satellite-based observations. Eight meridional transects and one zonal, ranging from 556 to 1139 km (300–615 nmi) long, were occupied through the fishing grounds between 1996 and 1999 aboard the NOAA ship *Townsend Cromwell* (TC)

(Fig. 1b). Hydrographic data through the water column were collected primarily with conductivity-temperature-depth (CTD) casts to 500 m at stations of 28 km (15 nmi) resolution; spacing was scaled to resolve the complex thermohaline frontal features (Roden, 1980). All casts utilized a SeaBird SBE 9/11 + CTD system equipped with a WetStar mini fluorometer for measuring in situ chloropigment (chlorophyll + phaeopigments) concentration; descent rates were 30 m min⁻¹ over the initial surface to 150 m, increasing to about 50-60 m min⁻¹ over the remaining cast to 500 m. Downcast CTD data were processed, binned into 2 m depth bins, and parameters derived using the SeaBird SEASOFT[©] software package v. 4.212. Contoured vertical sections (i.e. with respect to depth) of each desired parameter were generated with Matlab® v. 5.3 subroutines.

With the exception of the first cruise in 1996, discrete depth water samples were also collected on all of the surveys using a 12-place, CTD-mounted, rosette sampler and General Oceanics PVC Niskin bottles (2.5–10.0 L) for extracted pigment and inorganic macronutrient determinations. Niskin bottles were triggered onboard electronically at 500, 300, 200, 150, 125, 100, 80, 65, 50, 35, 20 m, and at the surface during the upcasts.

Chloropigment was measured in two ways: by *in vivo* fluorescence (CTD-mounted fluorometer) and by extracted fluorescence with a Turner Designs model 10-AU fluorometer. Samples for extracted pigments were drawn in dark 1-L high-density polyethylene (HDPE) bottles, vacuum filtered onto 47-mm-diameter, 0.7-µm Gelman TCLP glass-fibre filters, and extracted in 90% acetone (dark, -20°C) for 24–48 h. Chlorophyll *a* was corrected for interference by phaeopigments with acidification (Holm-Hansen *et al.*, 1965; Smith *et al.*, 1981). *In situ* chloropigment

Table 1. Towns	end Cromwell shipboard	l surveys and corre	esponding satellite	altimetry data	from TOPEX/POSEIDON.

Cruise	Dates	Latitude range (°N)	Longitude range (°W)	Transect length (km)	Corresponding TOPEX cycle	TOPEX cycle dates
TC 96-06 TC 97-03	8–12 May 1996 22–24 March 1997 5–7 April 1997	26°00′–32°00′ 26°00′–30°00′ 26°00′–31°00′	172°00′ 156°00′ 152°00′	667 444 556	134 166 168	3–13 May 1996 17–27 March 1997 27 March–6 April 1997
TC 97-04	30 April–4 May 1997 10–12 May 1997 12–14 May 1997	26°00′–34°00′ 29°00′ 24°00′–29°00′	172°00′ 172°00′–167°30′ 167°30′	889 500 556	170 171 171	26 April–5 May 1997 5–15 May 1997 5–15 May 1997
TC 98-05	24 April–1 May 1998 2–5 May 1998	23°00′–33°00′ 27°00′–32°00′	158°00′ 156°00′	1111 556	207 207	27 April–7 May 1998 27 April–7 May 1998
TC 99-05	27 April–1 May 1999	22°45′–33°00′	158°00′	1139	244	27 April–1 May 1999

concentrations were then calibrated against concurrent extracted uncorrected readings of total chlorophyll with a model I least squares linear regression $(r^2 = 0.72, \text{ Laws}, 1997)$. The high-resolution profiling fluorometer data provided the finest spatial resolution of chloropigment distribution and will be the primary biological measurement presented. Integrated chloropigment values were calculated for the upper 100 m using the 'trapezoid rule' on 5 m averaged depth bins (Laws, 1997). Chlorophyll a and other accessory pigments were also determined by high-performance liquid chromatography (HPLC) for samples collected along 158°W longitude in 1998. Samples for HPLC were drawn in 2-L translucent bottles, kept shielded from sunlight, filtered as above, folded into aluminium foil, and frozen in liquid nitrogen for transport to the laboratory for analysis using the methods described in Bidigare & Trees (2000). Fucoxanthin and peridinin were used as chemotaxonomic markers for identifying the presence of diatoms and dinoflagellates (Andersen et al., 1996; Bidigare & Ondrusek, 1996; Scharek et al., 1999).

Water samples for nutrient determination were drawn using clean Tygon tubing in 125-mL acid-washed HDPE bottles, each rinsed three times with sample prior to filling. Samples were immediately frozen without filtration and kept frozen until the day of analysis. All nutrient samples were analysed for dissolved inorganic nitrate + nitrite, phosphate, and silicate with a Technicon autoanalyser at the University of Hawaii School of Ocean and Earth Science and Technology (SOEST) Analytical Services Laboratory (Lukas & Karl, 1999). Data on the latter two nutrients are not presented here.

Information on currents along the transects was collected by continuous underway measurements with a 153-kHz hull-mounted RDI acoustic Doppler current profiler (ADCP) to a depth of about 350 m. Processing protocols followed the basic procedures described by Bahr *et al.* (1989) with the subroutines developed at the University of Hawaii as CODAS (Common Oceanographic Data Analysis System¹) (Firing *et al.*, 1994).

For satellite data, we used sea surface temperature (SST) from the National Oceanic and Atmospheric Administration's (NOAA) Advanced Very High-Resolution Radiometer (AVHRR), ocean colour from SeaWiFS, and most importantly, sea level anomaly (SLA) from the altimeter aboard TOPEX/POSEI-

DON (T/P). As detailed in Polovina et al. (1999), altimetry data were obtained from the 2-day Delayed Altimeter Data project of the NOAA Laboratory for Satellite Altimetry, a joint endeavour with the Naval Oceanographic Office and the Jet Propulsion Laboratory. The data are aggregated into 1° latitude intervals along the satellite track and expressed as SLAs relative to the mean altimetry from the first 3 years (1993– 1995) of the T/P mission; data are acquired about 2 days after the completion of a 10-day satellite cycle. The individual cycle data are smoothed, interpolated and gridded through a series of Generic Mapping Tools (GMT)² subroutines (Wessel & Smith, 1991). After adding a grid of equal dimensions containing the Levitus long-term mean dynamic height³ relative to 1000 m, a false colour contour map of dynamic height with an overlay of geostrophic current velocity vectors (calculated for the grid file of absolute altimetric values at 0.5° resolution) was created (Fig. 2). Altimeter data, representing the most recent cycle available prior to or early on during the field sampling period, were consulted and proved instrumental in establishing field sampling targets; subsequent cycles corresponding to the concurrent sampling period were used to help interpret the 2-D information acquired from the shipboard surveys.

RESULTS

Physical environment

The T/P altimeter maps (e.g. Fig. 2) illustrate the highly energetic STFZ as a broad region of large SLA gradients and high geostrophic current velocities meandering between 26° and 32°N latitudes, the region spatially corresponding to the swordfish fishing grounds. A pervasive field of mesoscale activity in various stages of formation and decay is seen to characterize the STFZ, with cyclonic eddies and meanders prevalent to the north of the strongest frontal currents and anticyclonic features to the south.

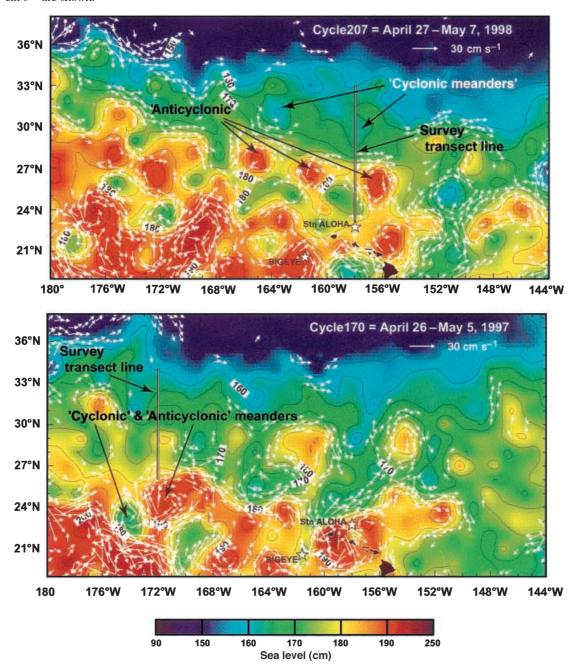
Recurrent patterns in the distribution of thermohaline, as well as biological (see below), properties observed at the fronts during the course of the present study provide new or corroborate previously reported

¹The public domain Common Oceanographic Data Analysis System (CODAS) software package is available at http://ilikai.soest.hawaii.edu/sadcp/

²The public domain Generic Mapping Tools (GMT) software package is available at http://www.soest.hawaii.edu/gmt/

³The Levitus data originates from the 1994 NODC World ocean atlas (CD-ROM data set), U.S. Department of Commerce, NOAA, National Environmental Satellite, Data, and Information Service (NESDIS).

Figure 2. Map of sea level height (with the Levitus long-term mean dynamic height at 1000 m added) from the altimeter aboard TOPEX/POSEIDON for (a) cycle 207, 27 April–7 May 1998 and (b) cycle 170, 26 April–5 May 1997. Highlighted vertical lines along (a) 158°W and (b) 172°W longitudes depict the concurrent hydrographic section sampled by the NOAA R/V *Townsend Cromwell*. Colour shading and 5 cm contours represent altimetry gridded at 0.1° resolution and a smoothing radius of 6.5°. Corresponding geostrophic current velocities (vectors) are presented for 0.5° spatial resolution; only velocities > 10 cm s⁻¹ are shown.



diagnostic characters associated with the SSTF and the STF. This characterization enables ready identification of the frontal presence and position from both satellite- and shipboard-based platforms. Of the eight me-

ridional transects conducted, only two surveys (1998 – 158°W, 1997 – 172°W longitudes) traversed both the SSTF and STF, a consequence of the considerable variability encountered in the temporal (interannual

and seasonal) latitudinal position and intensity of the fronts. We will focus therefore on the hydrography from these two transects to detail the salient properties that characterize the respective individual fronts and

adjacent waters. Vertical sections of temperature (°C), salinity (practical salinity scale), and density (σ_t) are presented for the 1998 – 158°W and the 1997 – 172°W surveys in Figs 3 and 4, respectively.

Figure 3. Meridional vertical section of (a) temperature (°C), (b) salinity, (c) density (σ_t kg m³), (d) *in situ* chloropigment (mg m⁻³), and (e) nitrate + nitrite (μ M) along 158°W longitude, 24 April–1 May 1998. White contour line in N-section depicts the 1 μ M N + N isopleth.

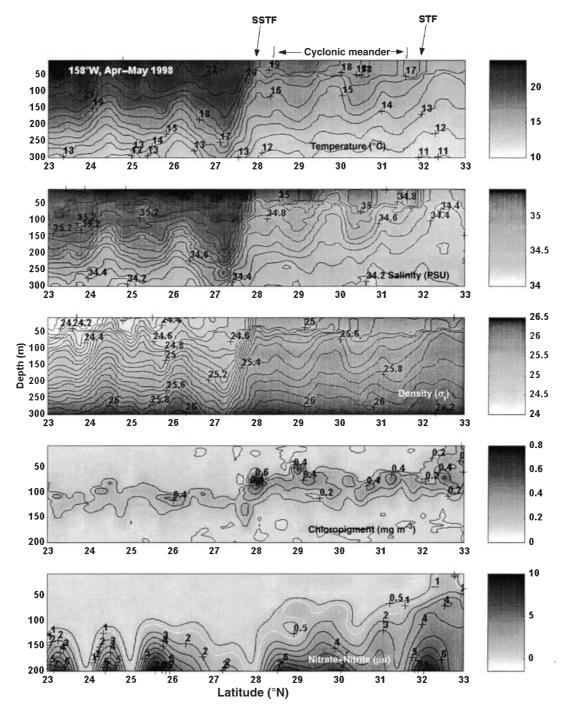
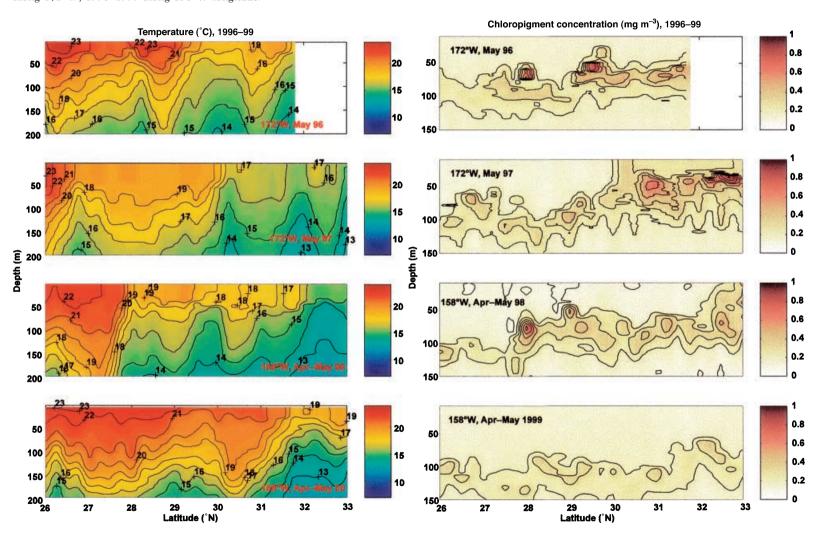


Figure 4. Comparative vertical sections of (a) temperature (°C) and (b) chloropigment (mg m⁻³) from annual surveys 1996–1999; 1996–1997 surveys conducted along 172°W, 1998–1999 along 158°W longitude.



The 1998 - 158°W meridional survey covered 1140 km (615 nmi), encountering the SSTF near 28°N latitude and the STF just north of 32°N latitude (Fig. 3). Cross-frontal thermohaline surface gradients were steepest to the south at the SSTF where gradients in temperature ($\triangle T$), salinity ($\triangle S$), and density $(\Delta \sigma_{\rm t})$ were observed at $\sim 3^{\circ}{\rm C}$ (50 km)⁻¹, ~ 0.7 $(50 \text{ km})^{-1}$, and $\sim 0.6 (50 \text{ km})^{-1}$, respectively. These surface gradients also formed a thin layer of increased hydrostatic stability at depth, a hydrographic characteristic of subtropical waters (Roden, 1972, 1980, 1981). Mixed layer depths typically extended to ~ 50 m. Embedded in the prevailing flow at the SSTF was a strong cyclonic meander (c. 100 km across) centred near 29°N. This mesoscale feature, which was evident in concurrent satellite altimetry (Fig. 2a), is seen in the vertical sections (Fig. 3) as alternating patterns in temperature and salinity through the region. An anticyclonic meander centred near 28°45'N latitude along the 172°W longitudinal survey was also traversed in 1996 (Fig. 4, top panels).

The 1997 survey along 172°W longitude covered 889 km (480 nmi) and traversed the SSTF in the vicinity of 26°-26.5°N latitude and the STF at 30°N latitude (Fig. 5). These fronts exhibited horizontal surface temperature gradients on the order of 3°C $(56 \text{ km})^{-1}$ and 2°C $(28 \text{ km})^{-1}$ for the SSTF and STF, respectively. In addition, a third front with a moderate surface frontal gradient of 1°C (28 km)⁻¹ was encountered to the north. This latter front, described by Lynn (1986) as the North Subtropical Front, is also a recurrent feature during spring in the southern half of the North Pacific Transition Zone (NPTZ). A zonal section along 29°N latitude between 179°W and 174°30′W longitudes, subsequently conducted after completion of the 172°W line, traversed a cyclonic meander identified from T/P imagery (Fig. 6). Strong vertical displacement of isotherms corresponding to the meander presence is observed.

In both of these surveys, and in the other surveys not detailed here, horizontal salinity and density gradients generally occurred at the surface coincident with temperature gradients; density fronts, however, were strongest to the south and diminished northward reflecting the increase in compensating horizontal temperature and salinity gradients. The SSTF could readily be identified by the surface outcrop of the 20°C isotherm, 35.0 isohaline, and 24.8 isopycnal, while the manifestation of the 17°C isotherm and 34.8 isohaline within surface gradients readily identified the STF, the latter characterization previously reported by Roden (1972, 1980). In each of the transects performed, the 'diagnostic isotherm and

isohalines' were common to the respective fronts. The seasonal thermo- and halo-clines shoal northward in a stepwise fashion with increments in alignment with frontal locations. As cooler, less saline and higher density water from north of the fronts subducts below warmer, more saline water to the south, localized secondary divergence and convergence also develop and appear in the vertical sections as uplifted and depressed isopleths marking distinct vertical shifts in water column properties.

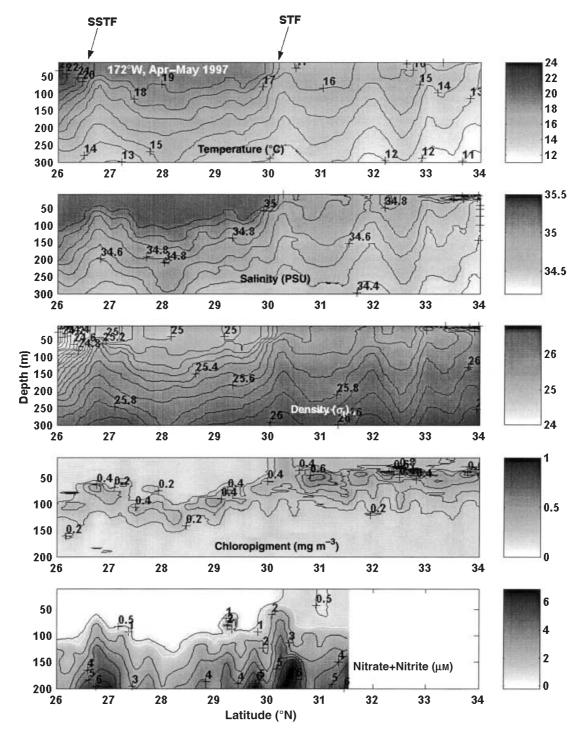
Considerable interannual variability in the latitudinal position and intensity of the SSTF and STF was observed between the 1996–1997 172°W, 1998–1999 158°W sections conducted at the same time each year (Fig. 4). A latitudinal shift in frontal positions of about 333 km was observed between each of the two pairs of comparable annual surveys.

As manifested in the ADCP data, currents along the sampled transects exhibited complex flow patterns (Fig. 7). Surface currents (depth-averaged over the upper 21–200 m) encountered along the 158°W and 172°W longitude lines averaged 22.8 cm s⁻¹ (SD = 14.9) and 23.0 cm s⁻¹ (SD = 12.3), respectively. At the SSTF, a strong zonal flow prevailed, exceeding 80 cm s⁻¹ on the 158°W transect and approaching 50 cm s⁻¹ on the 172°W line. Surface currents were generally much weaker at the STF where velocities peaked at about 37 cm s⁻¹ on both surveys.

Biological patterns

The vertical distribution patterns observed for chloropigments and macronutrients (nitrate + nitrite) varied in relation to the corresponding density (σ_t) structure, particularly with regard to pycnocline depth and strength of the 'subtropical high-stability layer' (i.e. hydrostatic stability) (Figs 3 and 4). Depths of the subsurface chloropigment maximum (SCM), a feature characteristic of subtropical waters, typically coincided with the nutricline depth (defined as the 1.0 μ M N isopleth). At the SSTF, the SCM strengthens and shallows to $\sim 60-80$ m as the thermocline and stability layer shoals to the upper euphotic zone on the cold side of the front. During the 1998 - 158°W and 1997 - 172°W transects, the SCM concentrations exceeded 1.0 mg m $^{-3}$ at 80 m and 0.6 mg m $^{-3}$ at 65 m, respectively. The STF marks the transition from low chloropigment (0.1 mg m⁻³), nutrient-depleted surface waters to the south to a more productive regime to the north where a twofold increase in surface chloropigment was observed (Figs 3 and 4) and can be readily monitored by remote-sensing of ocean colour (see Polovina et al., 2000, 2001).

Figure 5. Meridional vertical section of (a) temperature (°C), (b) salinity, (c) density (σ_t , kg m⁻³), (d) *in situ* chloropigment (mg m⁻³), and (e) nitrate + nitrite (μ M) along 172°W longitude, 30 April–5 May 1997. White contour line in N-section depicts the 1 μ M N + N isopleth.

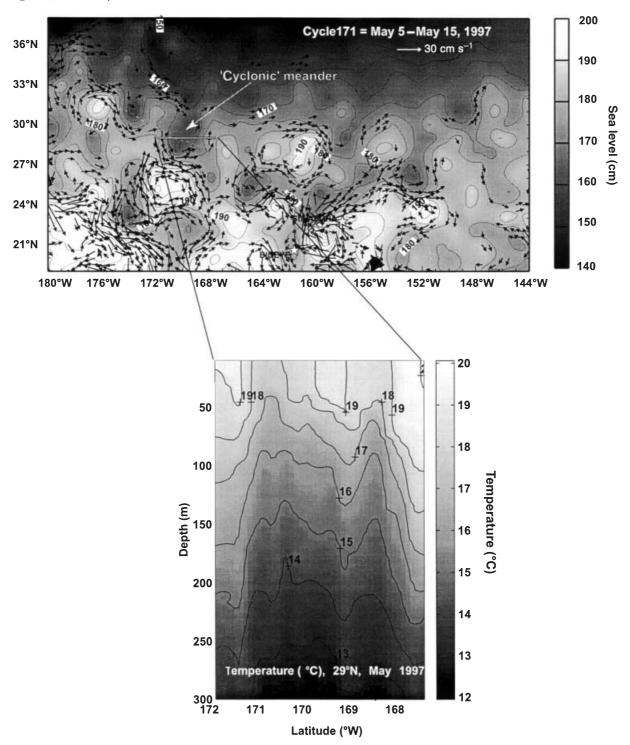


Integrated chloropigment levels exhibit distinct maxima in alignment with the SSTF and STF locations (Fig. 8), increases generally ascribed to increases

in the concentration and thickness of the SCM layer (Fig. 5). Chloropigment levels appeared especially amplified by vertical shear, compressed gradients,

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Figure 6. (a) Map of sea level height (with the Levitus long-term mean dynamic height at 1000 m added) from the altimeter aboard TOPEX/POSEIDON for cycle 171, 5–15 May 1997. Highlighted horizontal line along 29°N latitude depicts the concurrent hydrographic section sampled by the NOAA R/V *Townsend Cromwell*. Shading and 5 cm contours represent altimetry gridded at 0.1° resolution and a smoothing radius of 6.5°. Corresponding geostrophic current velocities (vectors) are presented for 0.5° spatial resolution; only velocities > 10 cm s⁻¹ are shown. (b) Zonal vertical section of temperature along 29°N longitude, 10–12 May 1997.



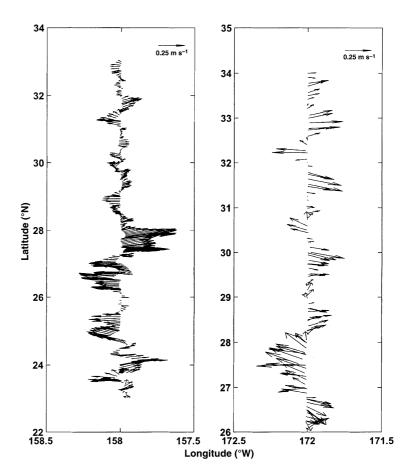


Figure 7. Schematic vector representation of estimated current velocities and direction along the (a) 158°W trackline, 24 April–1 May 1998 and (b) 172°W trackline, 30 April–5 May 1997. Measurements were averaged over the upper 21–100 m.

and vertical displacement of isopycnals (upwelling) induced by the presence of meanders embedded in the fronts sampled in 1996 and 1998.

Phytoplankton community structure, as deduced from HPLC accessory pigment determinations for the 1998 – 158°W survey, showed a dominance of recycled nutrient-based picophytoplankton (e.g. *Prochlorococcus* and *Synechococcus*) as observed previously for the subtropical North Pacific (Ondrusek et al., 1991; Letelier et al., 1993; Anderson et al., 1996; Bidigare & Ondrusek, 1996). With the flux of new nutrients in waters at the fronts were increases in the contribution of picoeukaryotic classes, such as prymnesiophytes (19'-hex-fucoxanthin) and pelagophytes (19'-but-fucoxanthin), particularly in the SCM (see Leonard et al., 2001).

DISCUSSION

A long-standing paradigm is that the North Pacific subtropical gyre is a very old, very large, homogeneous environment, with low seasonal and interannual variability, and one of the most oligotrophic marine ecosystems in the world (McGowan, 1974; Hayward

et al., 1983; Hayward, 1987; Venrick, 1990b). This perception has evolved principally from field studies conducted under stratified summer conditions, although limited winter sampling offered little indication of significant seasonal variability (Hayward et al., 1983). Up to now very limited effort has been expended during the winter and spring in the STFZ, when storm frequency is high and poor weather conditions in the region make sampling difficult. Venrick (1993) found evidence for enhanced growth among the deeper-dwelling phytoplankton species assemblage near 28°N 155°W during a single winter sampling. Our results highlight the seasonal STFZ fronts and the unique biological implications that characterize each feature.

During the spring, the SSTF could be consistently identified by the presence of surface outcropping of the 20°C isotherm and 35.0 isohaline. On the cold side of the front, there is a shoaling of the thermocline and with it the subtropical stability layer into the upper euphotic zone. This concept is important because in subtropical waters to the south, this density cap typically would reside in depths > 100 m (Roden, 1972, 1991; Bingham & Lukas, 1996) and is the principal

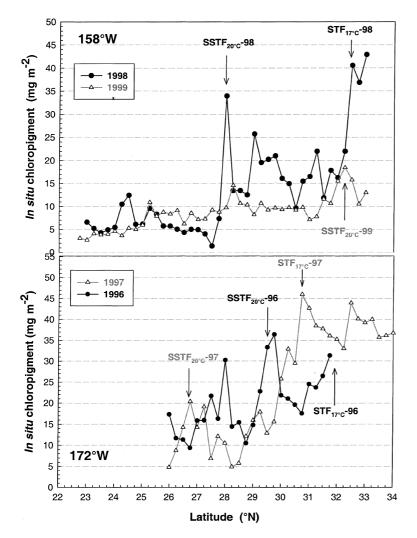


Figure 8. Along track *in situ* chloropigment (mg m⁻²) integrated over the upper 100 m depths for the (a) 1998–1999 158°W and (b) 1996–1997 172°W surveys.

force inhibiting the vertical flux of nutrients into the lighted surface waters (Mann & Lazier, 1991). Fluxes of nutrients into the euphotic zone in the subtropical gyre are probably as low as in any oceanic environment (Cullen, 1982). As a result, the SCM in the subtropics is normally found at about 120 m deep with chloropigment concentrations in the 0.2–0.4 mg m⁻³ range. By comparison, adjacent to the SSTF, the SCM intensifies and shoals to 60-80 m depths with the stability layer. As manifested in the 1997 zonal survey along 29°N (Fig. 6) and in 1997 on the 172°W and in 1998 on the 158°W surveys (Fig. 7), vertical displacement of isopycnals, associated with the embedded presence of frontal meanders further enhance pigment biomass (Bakun, 1996) as well as primary production in waters associated with the fronts (Leonard et al., 2001). Worth noting is that subsurface, increased pigment biomass, at the SSTF and from mesoscale perturbations, is not detectable by satellite remote sensing (ocean colour).

The spring STF is best characterized by the 17°C and 34.8 surface isotherm and isohaline, respectively; this is comparable with historical assessments by McGary (1956), Seckel (1968), and Roden (1980), who defined the STF as the surface expression of 18°C winter isotherm and 34.8 isohaline. For most of the sections encountered during the present study, the 17 and 18°C isotherms were both embedded among the frontal gradients; however, the 17°C character was most consistently present. A twofold increase in integrated chloropigment and surface chlorophyll a, namely the Transition Zone Chlorophyll Front (TZCF) (Polovina et al., 2001), was typically encountered on the cold side of the STF and can be attributed to the weakness in hydrostatic stability that facilitates the flux of nutrients into the lighted surface waters; hydrostatic stabilities are reportedly lower in the NPTZ than anywhere else in the open North Pacific (Roden, 1972, 1980, 1981, 1991). The absence of the strong density cap, fundamental to the subtropical water mass profile, marks the southern limit of the NPTZ. Although the positions of the STF and the TZCF coincided during the course of this study, these features are believed to be unique and are seen to diverge with changing season and possibly with an alternate climatological regime.

Of particular interest are the substantial increases observed in large dinoflagellates (with peridinin), along isopycnals at the SSTF interface, and diatoms (with fucoxanthin) centred on the embedded meander (Fig. 9). Increased primary productivity associated with larger eukaryotes may enhance the transfer efficiency to higher trophic levels; the rapid growth of diatoms generally ensures that they are the first to appear in the water column after inorganic nitrogenous nutrient enrichment (Jeffrey & Vesk, 1997). The presence of diatoms and dinoflagellates provides strong evidence for the generation of 'new production' in association with the physical forcing (Claustre, 1994; Claustre *et al.*, 1994).

Large excursions in variability of latitudinal position and frontal intensity of the SSTF and STF were observed between survey years. If we consider the time series of four cruises conducted at the same time each year 1996–1997 172°W, 1998–1999 158°W (Fig. 4), the SSTF occupied positions ranging over 5° of latitude (555 km or 300 nmi). Although we compare 2-D oceanographic sections here, evidence from satellite sensors suggests that large seasonal shifts of these frontal systems are observed on the basin scale; e.g. Kazmin & Rienecker (1996). Conceivably, the very strong 1998 El Niño and subsequent 1999 La Niña may likely have had a large role in observed patterns. Roden (1981) reported a change in intensity and

position of the STF between surveys conducted in 1974 and 1980; the STF was positioned 150 km farther south in 1980 and the density contrast was stronger. The southward shift was attributed to a southerly shift in the westerlies and storm tracks in the central North Pacific (Roden, 1981). More recently, Letelier *et al.* (2000) observed a southward meander of the SSTF to at least 22°30′N at 158°W during March–April 1997. Biological studies conducted at the CLIMAX site, at 28°N 155°W in close proximity to the present surveys, found low interannual variability in phytoplankton biomass and community structure in this ecosystem, although sampling was concentrated during summer (Hayward *et al.*, 1983; Venrick, 1990b).

Relationships between the physical environment and higher trophic levels as they relate to swordfish have been considerably more difficult to ascertain, primarily because of the difficulty in acquiring the necessary biological information for such an assessment. Commercial fisheries data suggest that swordfish are distributed relative to preferred thermal habitats and, especially, along temperature fronts (Podestá et al., 1993). This behaviour is thought to be a response to forage accumulation, migration cues, or energetic gains by riding currents (Olson et al., 1994). From a trophic standpoint, the increased biological productivity associated with the STFZ may set the framework for an enhanced feeding regime. Studies by Le Borgne (1981) and Longhurst & Herman (1981) have shown that standing crop of zooplankton are positively correlated with chlorophyll concentrations and that the depth of highest zooplankton

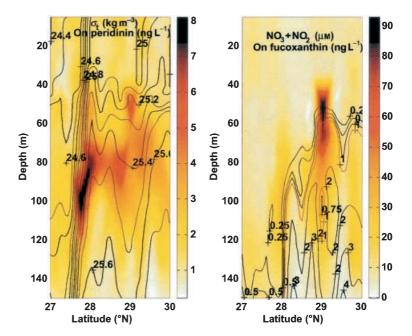


Figure 9. Vertical distribution of diagnostic accessory pigments: (a) peridinin (ng L^{-1}) and (b) fucoxanthin (ng L^{-1}) measured across the SSTF along 158°W long. False-colour images are illustrated with contours of density ($\sigma_{\rm t}$, kg mg⁻³) and N-nutrient input, respectively.

concentration coincides with the depth of the highest production rates; i.e. the depth of the thermo- and nutriclines. Accordingly, shoaling of the vertical thermal structure leads to layers of high zooplankton abundance that become feeding sites for predators.

Ongoing and published swordfish diet studies suggest opportunistic feeding on available surface-dwelling prey but identify a predilection for squid, particularly among fish sampled during the winter months of the fishing season (Toll & Hess, 1981; Stillwell & Kohler, 1985; Seki, 1993). Limited information from research surveys have suggested substantially higher squid, *Ommastrephes bartramii*, abundance occurring at regions adjacent to the cold side of the southern front of the STFZ. Correspondingly, swordfish catch rates are also highest in this vicinity along the same front during this time period. Shoaling of the thermocline is believed to concentrate swordfish and their prey closer to the ocean surface and thus more vulnerable to surface longline gear.

The spring STF system is also integral to a number of other pelagic fauna. Albacore tuna, Thunnus alalunga, and loggerhead sea turtles, Caretta caretta, exhibit strong affinity to the STFZ fronts (Laurs & Lynn, 1977; Polovina et al., 2000). Not surprisingly, the US commercial trolling and, now defunct, Japanese high seas driftnet fisheries targeted albacore tuna at the fronts in STFZ waters (Laurs et al., 1984; Nakano et al., 1993). Several Transition Zone shortlived 'food species' including the Pacific pomfret, Brama japonica, and the flying squid undergo extensive migrations to spawn in the STFZ (Shimazaki & Nakamura, 1981; Murata, 1990; Seki & Bigelow, 1993). These seasonally resident resources probably play a decisive role in the timing of peak fishing activity in the Hawaii-based fishery.

Finally, we used near real-time satellite altimetry to direct the field sampling for our studies on coupled physical-biological relationships at mid-ocean fronts and frontal systems in the Subtropical North Pacific. Shipboard measurements of thermohaline structure agreed surprisingly well with those inferred form T/P altimeter images, particularly in hindcasts, when the cycle data overlapped the sampling period. However, modest deviations in frontal position and intensity, observed in T/P altimetry from cycle to cycle, are quite substantial in relation to local time and space scales of shipboard surveys. Nevertheless, the forecasting capability offered by T/P images has enhanced our ability to optimize sampling strategy with more efficient use of valuable ship time. Improvements in our predictive capabilities through image analysis will come with time and continued applications.

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REFERENCES

Andersen R.A., Bidigare R.R., Keller M.D. & Latasa M. (1996) A comparison of HPLC pigment signatures and electron microscopic observations for oligotrophic waters of the North Atlantic and Pacific Oceans. *Deep-Sea Res. II* 43:517– 537.

Bahr F., Firing E. & Songnian J. (1989) Acoustic Doppler Current Profiling in the Western Pacific During the US-PRC TOGA Cruises 2, 3, and 4. Contrib. no. 89-0175, Data Rept. no. 005. Joint Institute for Marine and Atmospheric Research, University of Hawaii, Hawaii, p. 199.

Bakun A. (1996) Patterns in the Ocean. Ocean Processes and Marine Population Dynamics. California Sea Grant College Program, University of California, California, 323 pp.

Bidigare R.R. & Ondrusek M.E. (1996) Spatial and temporal variability of phytoplankton pigment distributions in the central equatorial Pacific Ocean. *Deep-Sea Res.* II (43):809–833

Bidigare R.R. & Trees C.C. (2000) HPLC phytoplankton pigments: sampling, laboratory methods, and quality assurance procedures. In: Ocean Optics Protocols for Satellite Ocean Color Sensor Validation, Revision 2. J. Mueller & G. Fargion (eds). NASA Technical Memorandum 2000–209966, pp. 154–161.

Bigelow K.A., Boggs C.H. & He X. (1999) Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fish. Oceanogr. 8:178–198.

Bingham F.M. & Lukas R. (1996) Seasonal cycles of temperature, salinity and dissolved oxygen observed in Hawaii Ocean Time-series. *Deep-Sea Res.* **43:**199–213.

- Claustre H. (1994) The trophic status of various oceanic provinces as revealed by phytoplankton pigment signatures. *Limnol. Oceanogr.* **39:**1206–1210.
- Claustre H., Kerhervé P., Marty J.C., Prieur L., Videau C. & Hecq J.-H. (1994) Phytoplankton dynamics associated with a geostrophic front: ecological and biogeochemical implications. J. Mar. Res. 52:711–742.
- Cullen J.J. (1982) The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a. Can. J. Fish. Aquat. Sci. 39:791–803.
- Fiedler P.C. & Bernard H.J. (1987) Tuna aggregation and feeding near fronts observed in satellite imagery. Cont. Shelf Res. 7:871–888.
- Firing J., Flament P., Knox R. & Firing E. (1994) Acoustic Doppler current profiler data from the R/V Moana Wave. cruises MW9010 (2 August to 9 September 1990) and MW9012 (9 November to 14 December 1990). SOEST Tech. Rep. 93-05:871.
- Hayward T.L. (1987) The nutrient distribution and primary production in the central North Pacific. Deep Sea Res. 34:1593–1627.
- Hayward T.L. & McGowan J.A. (1985) Spatial patterns of chlorophyll, primary production, macrozooplankton biomass, and physical structure in the central North Pacific Ocean. *J. Plankton Res.* 7:147–167.
- Hayward T.L., Venrick V.L. & McGowan J.A. (1983) Environmental heterogeneity and plankton community structure in the central North Pacific. J. Mar. Res. 41:711–729.
- Holm-Hansen O., Lorenzen C.J., Holmes R.W. & Strickland J.D. (1965) Fluorometric determination of chlorophyll. J. Cons. Int. Explor. Mer 30:3–15.
- Ito R.Y. & Coan. A.L. Jr (1999) U.S. swordfish fisheries of the North Pacific Ocean. In: Proceedings of the Second International Pacific Swordfish Symposium. G.T. Dinardo (ed.). NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-263, pp. 19–38.
- Ito R.Y., Dollar R.A. & Kawamoto K.E. (1998) The Hawaii-based longline fishery for swordfish, Xiphias gladius. In: Biology and Fisheries for Swordfish, Xiphias gladius. I. Barrett, O. Sosa-Nishizaki & N. Bartoo (eds). U.S. Department of Commerce. NOAA Technical Report NMFS 142:77–88.
- Jeffrey S.W. & Vesk M. (1997) Introduction to marine phytoplankton and their pigment signatures. In: Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods. S.W. Jeffrey, R.F.C. Mantoura & S.W. Wright (eds). France: UNESCO Publishing, pp. 37–84.
- Kazmin A.S. & Rienecker M.M. (1996) Variability and frontogenesis in the large-scale oceanic frontal zones. *J. Geophys. Res.* 101:907–921.
- Laurs R.M., Fiedler P.C. & Montgomery D.R. (1984) Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Res.* 31:1085–1099.
- Laurs R.M. & Lynn R.J. (1977) Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance and association with transition zone waters. Fish. Bull. US 75:795–822.
- Laws E. (1997) Mathematical Methods for Oceanographers: an Introduction. New York: John Wiley & Sons, Inc., 343 pp.
- Le Borgne R. (1981) Relationship between the hydrological structure, chlorophyll and zooplankton biomasses in the Gulf of Guinea. J. Plankton Res. 3:577–592.
- Leonard C.L., Bidigare R.R., Seki M.P. & Polovina J.J. (2001) Interannual mesoscale physical and biological variability

- in the North Pacific Central Gyre. Progr. Oceanogr.49: 227–244.
- Letelier R.M., Bidigare R.R., Hebel D.V., Ondrusek M., Winn C.D. & Karl D.M. (1993) Temporal variability of phytoplankton community structure based on pigment analysis. *Limnol. Oceanogr.* **38:**1420–1437.
- Letelier R.M., Karl D.M., Abbot M.R., Flament P., Freilich M., Lukas R. & Strub T. (2000) Role of late winter mesoscale events in the biogeochemical variability of the upper water column of the North Pacific Subtropical Gyre. J. Geophys. Res.
- Longhurst A.R. & Herman A.W. (1981) Do oceanic zooplankton aggregate at, or near, the deep chlorophyll maximum? J. Mar. Res. 39:353–356.
- Lukas R. & Karl D.M. (1999) Hawaii Ocean Time-series (HOT). A decade of interdisciplinary oceanography. SOEST Technical Rep 99-05, CD-ROM.
- Lynn R.J. (1986) The Subarctic and northern Subtropical Fronts in the eastern North Pacific Ocean in spring. *J. Phys. Oceanogr.* **16**:209–222.
- Mann K.H. & Lazier J.R.N. (1991) Dynamics of Marine Ecosystems. Biological—Physical Interactions in the Oceans. Cambridge: Blackwell Scientific Publications, 466 pp.
- McGary J.W. (1956) Mid-Pacific oceanography, middle latitude waters, Jan–March 1954. Spec. Sci. Rep. Fish. 180:173.
- McGowan J.A. (1974) The nature of oceanic ecosystems. In: The Biology of the Oceanic Pacific. C.B. Miller (ed.). Corvalis: Oregon State University Press, pp. 9–28.
- Murata M. (1990) Oceanic resources of squids. Mar. Behav. Physiol. 18:19–71.
- Nakano H., Okada K., Watanabe Y. & Uosaki K. (1993) Outline of the large-mesh driftnet fishery of Japan. In: Symposium on Biology, Distribution and Stock Assessment of Species Caught in the High Seas Driftnet Fisheries in the North Pacific Ocean. J. Ito, W. Shaw & R.L. Burgner (eds). Bull. Internat. N. Pac. Fish. Comm. 53:25–38.
- Olson D.B., Hitchcock G.L., Mariano A.J., Ashjian C.J., Peng G., Nero R.W. & Podestá G.P. (1994) Life on the edge: marine life and fronts. *Oceanography* **7:**52–60.
- Ondrusek M.E., Bidigare R.R., Sweet S.T., Defreitas D.A. & Brooks J.M. (1991) Distribution of phytoplankton pigments in the North Pacific Ocean in relation to physical and optical variability. *Deep-Sea Res.* 38:243–266.
- Podestá G.P., Browder J.A. & Hoey J.J. (1993) Exploring the association between swordfish catch rates and thermal fronts on U.S. longline grounds in the western North Atlantic. Continental Shelf Res. 13:253–277.
- Polovina J.J., Kleiber P. & Kobayashi D.R. (1999) Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993–1996. Fish. Bull. US 97:132–143.
- Polovina J.J., Kobayashi D.R., Parker D.M., Seki M.P. & Balazs G.H. (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts spanning longline fishing grounds in the central North Pacific, 1997–1998. Fish. Oceanogr. 9:71–82.
- Polovina J.J., Howell E., Kobayashi D.R. & Seki M.P. (2001) The Transition Zone Chlorophyll Front, a dynamic, global feature defining migration and forage habitat for marine resources. *Progr. Oceanogr.* **49:**469–483.
- Roden G.I. (1972) Temperature and salinity fronts at the boundaries of the Subarctic-Subtropical Transition Zone in the Western Pacific. J. Geophys. Res. 27:7175–7187.

- Roden G.I. (1980) On the Subtropical Frontal Zone north of Hawaii during winter. *J. Phys. Oceanogr.* **10:**342–362.
- Roden G.I. (1981) Mesoscale thermohaline, sound velocity and baroclinic flow structure of the Pacific Subtropical Front during the winter of 1980. J. Phys. Oceanogr. 11:658– 675.
- Roden G.I. (1991) Subarctic-subtropical transition zone of the North Pacific: large-scale aspects and mesoscale structure. In Biology, Oceanography and Fisheries of the North Pacific Transition Zone and the Subarctic Frontal Zone. J.A. Wetherall (ed.). NOAA Technical Rep NMFS 105:1–38.
- Sakagawa G.T. (1989) Trends in fisheries for swordfish in the Pacific Ocean. In: Planning the Future of Billfishes. Research and Management in the 90s and Beyond. R.H. Stroud (ed.). Mar. Recr. Fish. 13:61–79.
- Scharek R., Latasa M., Karl D.M. & Bidigare R.R. (1999) Temporal variations in diatom abundance and downward vertical flux in the oligotrophic North Pacific gyre. *Deep-Sea Res.* 46:1051–1075.
- Seckel G.R. (1968) A time sequence oceanographic investigation in the North Pacific tradewind zone. *Trans. Am. Geo*phys. *Union* 49:377–387.
- Seki M.P. (1993) Trophic relationships of Ommastrephes bartramii during winter migrations to subtropical waters north of the Hawaiian Islands. In: Recent Advances in Cephalopod Fisheries Biology. T. Okutani, R.K. O'Dor & T. Kubodera (eds). Tokyo, Japan: Tokai University Press, pp. 523–529.
- Seki M.P. & Bigelow K.A. (1993) Aspects of the life history and ecology of the Pacific pomfret, Brama japonica, during winter occupation of the Subtropical Frontal Zone. In: INPFC Symposium on Biology, Distribution, and Stock Assessment of Species Caught in the High Seas Driftnet Fisheries in the North

- Pacific Ocean, Vancouver, Canada. J. Ito, W. Shaw & R.L. Burgner (eds). Bull. Internat. N. Pac. Fish. Comm. 53:273–283.
- Shimazaki K. & Nakamura S. (1981) Ecological studies of the pomfret (*Brama japonica* Hilgendorf). I. The seasonal distribution pattern and ecological considerations. *Res. Inst. North Pac. Fish.*, *Hokkaido Univ.*, **Special Volume:**91–103 [In Japanese with English abstract].
- Smith R.C., Baker K.S. & Dustan P. (1981) Fluorometric techniques for the measurement of oceanic chlorophyll in the support of remote sensing. SIO Ref. 81–17. Scripps Institution of Oceanography, University of California, San Diego, CA, 14 pp.
- Stillwell C.E. & Kohler N.E. (1985) Food and feeding ecology of the swordfish *Xiphias gladius* in the western North Atlantic Ocean with estimates of daily ration. *Mar. Ecol. Prog. Ser.* 22:239–247.
- Toll R.B. & Hess S.C. (1981) Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Florida Straits. *Fish. Bull.* US **79:**765–774.
- Venrick E.L. (1988) The vertical distributions of chlorophyll and phytoplankton species in the North Pacific central environment. J. Plankton Res. 10:987–998.
- Venrick E.L. (1990a) Mesoscale patterns of chlorophyll *a* in the central North Pacific. *Deep-Sea Res.* **37:**1017–1031.
- Venrick E.L. (1990b) Phytoplankton in an oligotrophic ocean: species structure and interannual variability. *Ecology* 7:1547–1563.
- Venrick E.L. (1993) Phytoplankton seasonality in the central North Pacific: the endless summer reconsidered. *Limnol. Oceanogr.* 38:1135–1149.
- Wessel P. & Smith W.H.F. (1991) Free software helps map and display data. EOS. Trans. Am. Geophys. Union 72:441.